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# Mechanosensory Neurons With Bend- and Osmo-sensitivity in Mouthpart Setae From the Spiny Lobster *Panulirus argus*

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**Abstract.** The mouthparts of the spiny lobster *Panulirus argus* hold primarily two types of setae—simple setae and cuspidate setae. Mechanosensory neurons from these setae were examined by electrophysiological recordings. The population of simple setae contained two types of mechanosensory neurons: displacement-sensitive neurons, which responded to deflection at the setal base; and bend-sensitive neurons, which responded to bending of the setal shaft. Displacement-sensitive neurons, in general, responded phasically and only during actual displacement. Typically, their response changed with alteration of the direction, amplitude, and velocity/acceleration of the mechanical stimulus. Bend-sensitive neurons, in general, responded phaso-tonically and carried information on the direction and region of bending. This is the first experimental demonstration of bend sensitivity for arthropod setae. Cuspidate setae contain highly sensitive mechanosensory neurons; however, due to the rigid nature of these setae, whether they were bend sensitive or displacement sensitive could not be determined, and they were thus called "tactile neurons." Bend-sensitive neurons, but not displacement-sensitive neurons or tactile neurons, showed graded responses to changes in osmolarity. The osmosensitivity of these neurons could mediate behavioral responses to changes in the osmolarity of seawater or food.

## Introduction

Because they are completely covered by an exoskeleton, crustaceans need specialized sensors to detect external stimuli. These specializations, called setae, are hollow, hairlike extensions of the cuticle that contain the dendrites of the sensory neurons. Individual setae of aquatic crustaceans are either mechanosensory, chemosensory, or bimodal (both mechanosensory and chemosensory), the latter being the most common type based on morphological evidence (Schmidt and Gnatzy, 1984; Derby, 1989; Schmidt, 1989; Cate and Derby, 2001, 2002a, 2002b; Garm *et al.*, 2003). Crustaceans have been shown to respond behaviorally to changes in the osmolarity of their surroundings (Jury *et al.*, 1994; Dufort *et al.*, 2001); while the sensory structures behind this behavior are unknown, there are indications that the setal mechanoreceptors may sense osmotic changes (Tazaki, 1975).

Unimodal mechanosensory setae are located on the dorsal side of the carapace and abdomen and on the antennae of many decapod crustaceans. They are typically plumose (featherlike) in shape, innervated by one to four mechanosensory neurons, and specialized for detecting waterborne vibrations (Wiese, 1976; Vedel and Clarac, 1976; Tautz *et al.*, 1981; Vedel, 1985). They are sensitive to displacement, being responsive to movements of the entire seta around the basal membranous region, and can respond to displacements as small as 0.01 degrees (Wiese, 1976). Moreover, they respond most strongly to displacement in one direction, usually perpendicular to the outgrowths of the seta. Equipped with fields of these setae, each with a different directionality, animals can obtain detailed information about the location of the source of the vibrations.

Bimodal setae with mechanosensitivity have been experimentally demonstrated for a variety of setal types on the pereiopods and antennae of decapods (Shelton and Laverack, 1970; Hatt and Bauer, 1980; Altner *et al.*, 1983; Cate and Derby, 2001, 2002a, 2002b; Schmidt *et al.*, 2003).

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These mechanosensory neurons are believed to be displacement-sensitive, but little is known about their sensory properties such as directionality or response to changes in velocity.

Decapod crustaceans are known to have flexible feeding behavior. They can change how their mouthparts are used in feeding, depending on the nature—especially the size—of the prey item (Greenwood, 1972; Caine, 1975a, 1975b; Gerlach *et al.*, 1976; Kunze and Anderson, 1979; Schembri, 1982; Hunt *et al.*, 1992; Johnston, 1999; Garm and Høeg, 2001; Garm *et al.*, 2003; Garm, 2004). Moreover, crustacean mouthparts are known to have a high density of setae with a great diversity in external morphology (Schembri, 1982; Stemhuis *et al.*, 1998; Garm and Høeg, 2000; Coelho *et al.*, 2000), and the sparse morphological evidence suggests that most are bimodal mechanoreceptors and chemoreceptors (Paffenhöfer and Loyd, 2000; Garm *et al.*, 2003). To modify their feeding behavior, therefore, crustaceans are likely to acquire tactile information about the texture and shape of food while it is being handled by the mouthparts. Most of this information probably comes from the setae on the maxillipeds, since these mouthparts perform most of the manipulation and orientation of prey items during handling.

In this study, we have tested the hypothesis that mechanosensory neurons in the mouthpart setae of decapod crustaceans provide tactile information important for controlling feeding behavior. We have used the Caribbean spiny lobster *Panulirus argus* (Latreille, 1804) because it is an established model animal for crustacean sensory biology (Derby, 2000; Derby *et al.*, 2001; Harrison *et al.*, 2001; Ache, 2002; McClintock and Xu, 2002), and because its setae are large and thereby accessible for experimental work. Our focus is on the mandibular palp, the medial rim of the basis of maxilla 1 and maxilliped 1, the propodus and dactylus of the endopod of maxilliped 2, and the dactylus of the endopod of maxilliped 3. These structures are often in direct contact with prey during food manipulation (Garm, 2004), and thus are likely to have sensory functions; moreover, they are of sufficient size for convenient experimental manipulation. We examined the sensitivity of these neurons to setal displacement (deflection at their insertion), setal bending (deflection along their shaft), and osmotic changes in the seawater around them.

## Materials and Methods

### *Video recordings*

Adult male and female spiny lobsters, *Panulirus argus*, with carapace lengths of 45–90 mm, were obtained from Bermuda and kept in a 300-l aquarium at Danmarks Akvarium in Copenhagen. The video recordings were made in 50-l aquaria. Both systems had running seawater at 24 °C. For the recordings, the animals were fed mussels, fish meat, krill, and squid. A SONY DXC 950P color (Y/C) 3CCD camera equipped with a Micronikkor 105-mm macro lens was placed outside the aquarium and enabled 5-$\mu$m resolution. Recordings were made on PAL super VHS. Light was obtained from a 120-W bulb. Representative images of mouthpart movements were captured with a time resolution of 20 ms (50 images/s) using the frame grabber card DVRaptor from Canopus; the images were imported into CorelDraw 10.0, with a resolution of 720 × 564 pixels.

### *Electrophysiology*

Spiny lobsters, *Panulirus argus*, with carapace lengths of of 40–80 mm, were captured in the Florida Keys and maintained in two 400-l aquaria with artificial seawater (Instant Ocean, Aquarium Systems, Mentor, OH) at 23–28 °C, and fed shrimp and squid. Mouthparts examined in this study included the mandibular palp ($n = 4$), basis of maxilla 1 ($n = 2$), basis of maxilliped 1 ($n = 6$), endopod of maxilliped 2 ($n = 10$), and endopod of maxilliped 3 ($n = 21$). Between one and four neurons were studied per appendage. To gain access to the nerve bundles and artery of the various mouthparts, one of the appendages was ablated immediately before each experiment and dissected in cold lobster saline (gram/liter: 28 NaCl, 0.75 KCl, 3.4 $MgCl_2 \cdot 6H_2O$, 2.5 $CaCl_2 \cdot 2H_2O$, 3 $Na_2SO_4$, 0.3 glucose, 0.72 HEPES). For maxilliped 3, both the dactylus and propodus were removed from the endopod. The cuticle was removed from the propodus, and after the apodeme was cut at its insertion onto the dactylus, the muscle was gently removed with forceps. This dissection left behind only the principal artery flanked by the major nerve to the appendage. The artery and nerve bundle were separated from each other with a pair of fine tungsten needles, and the nerve was divided into four to six bundles. For the mandibular palp and endopod of maxilliped 2, the procedure was similar, although the endopod of maxilla 2 was cut at the merus-carpus joint, and the nerve in the carpus was used instead. For maxilla 1 and maxilliped 1, the basis was cut from the limb, and the cuticle was removed from the proximal half. In these limbs, only a small amount of muscle and connective tissue had to be removed to reveal the nerve and artery. When maxilla 1 or maxilliped 1 was used, the lobster was anesthetized on ice before dissection. Even though involved in food handling, the basis of maxilla 2 was not examined due to its small size.

After the dissection, the preparation was secured in a stimulating-recording chamber made of two petri dishes separated by a dental-wax barrier (Fig. 1A). The preparation was secured in the wax such that its two parts were bathed in different solutions. The distal part of the preparation, which housed undissected cuticle and setae, was situated in a stimulating dish that contained artificial seawater (gram/liter: 24.7 NaCl, 0.66 KCl, 4.7 $MgCl_2 \cdot 6H_2O$, 1.9

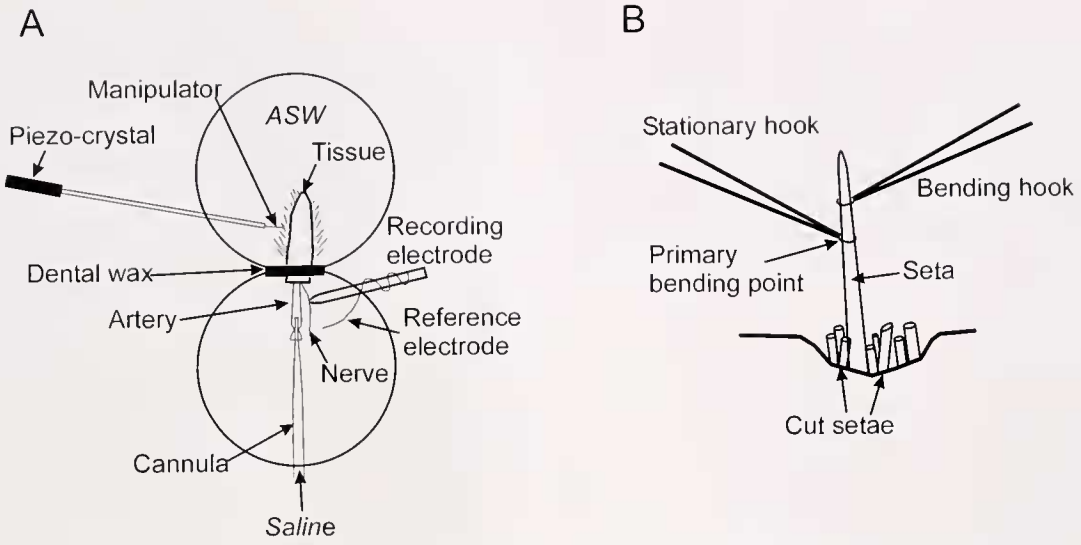


**Figure 1.** Experimental setup. (A) Schematic overview of the stimulating-recording chamber, showing how mechanical stimuli were applied with a piezoelectric-crystal-controlled probe. (B) Stimulation of a bend-sensitive cell. Neighboring setae were removed to allow space for stimulation of the seta innervated by the neuron of interest. This seta was bent around the attachment of a stationary hook. The bending hook was moved either by a piezoelectric crystal (see A) or by hand.

$CaCl_2 \cdot 2H_2O$, 6.3 $MgSO_4 \cdot 7H_2O$, 0.18 $NaHCO_3$); the proximal part, which contained the exposed nerve and artery, was situated in a recording dish that contained saline. After the wax barrier was sealed, the artery was cannulated and perfused with pressurized, oxygenated lobster saline at a rate of 0.4–1.1 ml/min (see Derby, 1995, for more details). The time from ablation of the mouthpart to perfusion was 10–15 min, and nerve recordings were initiated 15 min later.

Electrophysiological recordings were made *en passant* with fine-tipped extracellular suction electrodes (Derby, 1995). To determine whether the recording included mechanosensory neurons, a probe was used to brush the setae. If neural responses were detected, the seta innervated by the active neuron was identified by stimulating progressively smaller areas with the probe. The neighboring setae were then removed with a pair of scissors to ensure space for the micromanipulators and to ensure free movements of the seta of interest (Fig. 1B).

Two types of mechanical stimulation were presented—displacement and bending. Displacement is defined as moving the setae, with no apparent bending of the setal shaft itself, so that the angle between the base of the seta and the cuticle at its socket changes. Bending is defined as a deflection in the setal shaft, without any detectable displacement at its base. To examine displacement sensitivity, the seta was attached to a small tungsten hook, which in turn was connected to a piezoelectric crystal *via* an extension arm (Fig. 1A). Movement of the crystal was effected by applying 50–500 V, either in square or triangular pulses, using a wave generator amplified by a high-voltage DC amplifier. This provided movements ranging in amplitude from 0.12–1.2 mm measured with a micrometer scale bar. Simply attaching the hook to a simple seta resulted in no detectable alteration of the movements. To ensure that no force was applied in other than the direction of displacement, the hook moved freely along the setal shaft. This had the side effect that the angular velocity of the displacement was not constant, but declined within a single displacement following the equation: $\tan \alpha = D/L$, where $\alpha$ is the angle of displacement, $D$ is the distance traveled by the hook, and $L$ is the distance from the socket of the seta to the initial attachment point of the hook. This also meant that the two parameters, velocity and acceleration, could not be separated in our experiments. This coupling was enhanced by the failure of the hook to attain maximum velocity instantaneously; rather there was a period of acceleration, which was most significant when square signals were used. In effect the displacements started with a short period of acceleration to maximum velocity, then slowly decelerated until the direction reversed.

A change in the velocity/acceleration and amplitude of the stimulus was accomplished by changing the voltage and duration of the electrical signal from the wave generator. In these tests, triangular stimuli were used. When the velocity/acceleration sensitivity was tested, the amplitude was fixed at either 0.48 mm (200 V) or 0.72 mm (300 V), and stimulus duration was then varied using a stimulus frequency range of 1–10 Hz. When amplitude sensitivity was tested, the velocity/acceleration was fixed by using half the stimulation duration when doubling the voltage. Stimuli were presented

continuously for 15 s. Most displacement-sensitive neurons were also tested for bend sensitivity.

To examine bend sensitivity, one hook was situated at the place of desired bending, and the distal part was then moved to an angle of about 45° by either a handheld needle or a hook connected to a piezoelectric crystal (Fig. 1B). The neurons were also tested for their sensitivity to bending proximally relative to the holding point. All bend neurons were tested for displacement sensitivity by using maximum amplitude as described above.

When testing directionality, both displacement and bending were presented in four directions: distally (towards the tip of the appendage), proximally (away from the tip of the appendage), and medially and laterally (to the left and to the right of the appendage). Four displacement-sensitive and four bend-sensitive neurons were tested for the persistence of their response after the distal half of the seta was removed with a pair of scissors.

Because cuspidate setae and their reduced socket are very rigid, they could not be moved by the crystal, but only by a handheld needle. Thus, displacement and bending could not be reliably separated.

Sensitivity to changes in osmolarity was tested by placing the appendage in a tube with full-strength artificial seawater (*i.e.* 3.5%) flowing at 5 ml/min. The seawater was then exchanged with a 8-s pulse of either deionized water or a concentration series of artificial seawater from 1.75%–5.25% (*i.e.*, 50%–150% full-strength seawater) made by changing the concentration of NaCl. The concentration series was presented in steps first from 100% down to 50% and then from 100% up to 150%, with intertrial time intervals of 1 min. Three of each neuron type were also tested with deionized water for 5–15 min.

Each recording was made for 10 s with a sampling frequency of 56 kHz using Axoscope 9.0 software (Axon Instruments, Inc., Union City, CA). Spike sorting and quantification were performed using Datapac 2000 software (RUN Technologies, Mission Viejo, CA). All spikes for a given stimulation were used when analyzing both the number of spikes per stimulation and the interspike interval during a single stimulation.

## Results

The results are summarized in Tables 1 and 2. Recordings were obtained from neurons innervating two types of setae—simple and cuspidate (Fig. 2A, B). None of the neurons showed any spontaneous activity. Simple setae contained neurons that appeared to belong to either of two categories (Tables 1 and 2, Fig. 3). The first were displacement-sensitive neurons that responded to deflection of the entire seta at its socket. The second were bend-sensitive neurons that responded to bending of the setal shaft; a few of these neurons also gave small responses when displaced, presumably because of slight concomitant bending upon being displaced. The video recordings showed that bending does occur during food manipulation (Fig. 2C, D; supplementary video clips can be viewed at <http://www.mbl.edu/BiologicalBulletin/VIDEO/BB.video.html>).

The cuspidate setae contained neurons sensitive to the slightest movements of the seta, but since these neurons could not be stimulated in a controlled manner, they are referred to as "tactile neurons."

### *Displacement-sensitive neurons*

Displacement-sensitive neurons displayed phasic responses, spiking only during the actual setal displacement (Fig. 3A). None of the neurons responded to bending, and all of the neurons continued to respond to displacements after the distal half of their seta was removed. They were differentially sensitive to the direction, velocity, and amplitude of displacement, as described below.

Half of the displacement neurons (9 of 18 tested) showed directional sensitivity; in most cases, they responded much more strongly (*i.e.* with more spikes) to one of the four directions (Fig. 4). The "best" direction varied among the nine neurons, but distal and proximal displacement was most frequently the best direction. Only one neuron gave most spikes to lateral displacement, and no neuron responded most strongly to medial displacement. Some responded exclusively to displacement in one direction, but 7 of 9 neurons responded to two or more directions (Fig. 4). There was no significant difference between the number of

**Table 1**

*Number of cells tested for each stimulation parameter or combination of parameters*

| Type | Dir[1] | Amp[2] + Vel[3] + Dir | Amp + Vel | Amp + Dir | Vel + Dir | Region[4] | Region + Dir |
|---|---|---|---|---|---|---|---|
| Displace | 6 | 2 | 4 | 4 | 6 | — | — |
| Bend | 4 | — | — | — | — | 4 | 6 |

[1] Dir, Direction: Seta was bent or displaced in four directions (proximal, distal, medial, lateral).
[2] Amp, Aplitude: Seta was displaced with a series of amplitudes ranging from 0.2–1.2 mm.
[3] Vel, Velocity/Acceleration: Seta was displaced with a series of velocities/accelerations up to 12 mm/s.
[4] Region: Seta was bent at different regions along the shaft.

**Table 2**

*Summary of sensitivity of mechanosensory neurons*

| Setae type | Location | Modality | # of Cells tested | Responding to deionized water | Responding after cut midways | Directional sensitivity[1] | Amplitude sensitivity[2] | Velocity sensitivity[3] | Region sensitivity[4] |
|---|---|---|---|---|---|---|---|---|---|
| Cuspidate | Mx1 | "Tactile" | 2 | | | | | | |
| | Mxp2 | "Tactile" | 4 | 0/1 | 1/1 | | | | |
| | Mxp3 | "Tactile" | 4 | 1*/1 | 1/1 | | | | |
| Simple | Mdp | Bend | 2 | | | 2/2 | | | 1/2 |
| | | Displace | 3 | 0/1 | | 2/3 | 1/1 | 2/2 | |
| | Mxp1 | Bend | 5 | | 0/1 | 0/1 | | | 1/1 |
| | | Displace | 3 | | 1/1 | 1/2 | | | 1/1 |
| | Mxp2 | Bend | 6 | 4/4 | 0/3 | 2/3 | | | 4/4 |
| | | Displace | 6 | 0/3 | 2/2 | 1/3 | 1/1 | 3/3 | |
| | Mxp3 | Bend | 12 | 7/7 | | 2/4 | | | 2/3 |
| | | Displace | 21 | 0/5 | 1/1 | 5/10 | 6/6 | 6/6 | |

Responses are given as *x/y*, where *x* out of *y* tested cells responded to changes in the given parameter.

[1] Cell produced more spikes when stimulated in some directions than others.

[2] Cell produced more spikes when stimulated with higher amplitudes.

[3] Cell produced shorter interspike intervals when stimulated at higher maximum velocity/acceleration.

[4] Cell produced more spikes when the seta was bent at certain regions along the shaft than others.

* Cell responded only after the distal half of seta was cut off.

spikes produced per displacement of nondirectional neurons and directional neurons when displaced in their "best" direction (Students *t*-test, $P > 0.2$).

Displacement neurons were also amplitude sensitive (Table 2, Fig. 5). Greater amplitudes of displacement caused more spiking activity. This relationship is highly linear, with a slope of about 5; that is, a log increase in stimulus amplitude causes a 5-fold increase in the number of spikes (Fig. 5A). The mean spike interval did not correlate with stimulus amplitude (Fig. 5B). The neurons had a high threshold, and the setae that they innervated had to be moved some distance before they responded. Although we did not precisely measure the amplitude or angle of displacement at threshold, we estimated from microscopy that it was 0.15–0.20 mm, equal to 4–6° for a 2-mm-long seta. The threshold amplitude did not seem to change with higher stimulus velocity.

Velocity/acceleration was a third parameter influencing the response of the displacement neurons (Fig. 6). Increasing the maximum velocity of displacement caused an increased response magnitude, reflected as a decrease in mean interspike interval in all 12 tested neurons. Since most neurons gave a constant number of spikes, the spike trains were shorter at higher velocities/accelerations. When the maximum velocity was doubled, the mean interspike interval declined by 39% ± 6% (SEM), $n = 12$. In a few cases, there was a significant linear correlation between the maximum velocity and the mean interspike interval (example given in Fig. 6). At low velocities, no spikes were produced when the seta returned to its original position, but at higher velocities, one spike was occasionally produced during the return to the resting position of the seta.

Displacement neurons did not respond to changes in the osmolarity of the medium around the setae (Table 2). They did not respond to pulses of deionized water, and when bathed in deionized water, they continued to respond normally to displacements for at least 15 min. In one neuron, the cuticle was removed by cutting the seta, first midway up the shaft and subsequently even more proximally, and this neuron continued to respond to displacements and showed no response to deionized water.

### *Bend-sensitive neurons*

Bend-sensitive neurons generally gave phaso-tonic responses to bending of the setal shaft in that they continued to spike during bending sustained for many seconds (Fig. 3C). During such a prolonged period of bending, the neurons adapted to the stimulus and their firing frequency declined (Fig. 7). The rate of adaptation varied greatly, as indicated by the large standard error of the mean in firing rate over the various time intervals.

Of 10 bend neurons, 6 showed directional sensitivity (Table 2, Fig. 8). Like most of the directional displacement neurons, bend neurons did not respond exclusively to bending in one direction, but generally one direction produced a

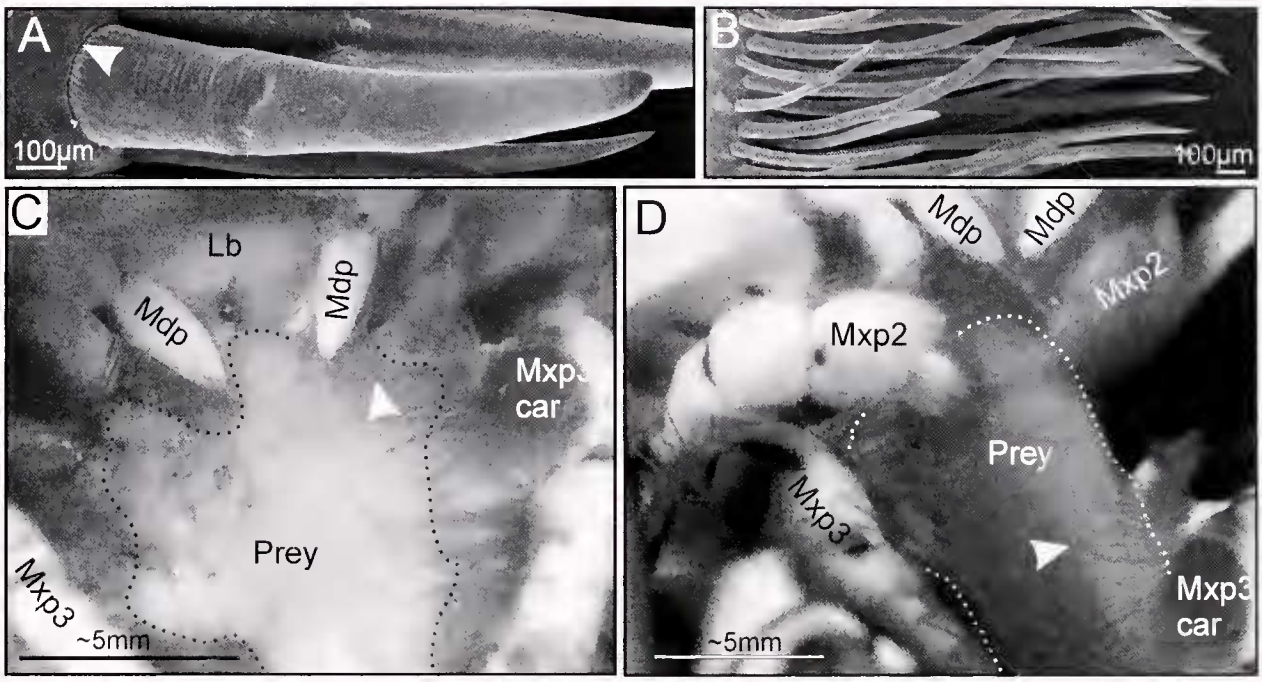


**Figure 2.** Morphology of the setae: scanning electron micrograph (SEM) and video images. (A) SEM image of a stout cuspidate seta from the endopod of maxilliped 2; the arrowhead indicates the very reduced socket of the seta. (B) SEM image of simple setae from the basis of maxilliped 1. (C, D) Video still images taken *ca.* 1 s apart showing a simple seta (arrowhead) that is from the carpus of maxilliped 3 (Mxp3 car) and bends during food manipulation. The seta is almost straight before prey contact (C) but bends in the distal half when contact is made (D). The broken line indicates the prey held by the mouthparts. car = carpus, Lb = labrum, Mdp = mandibular palp, Mxp2 = maxilliped 2, Mxp3 = maxilliped 3.

phaso-tonic high-frequency response, while other directions produced phasic responses and lower response rates (Fig. 8). Eight of the ten neurons tested responded unequally to bending at different regions in that they only responded to bending of the distal half of the seta (Fig. 9), but the experimental setup did not allow for precise location of the most sensitive region. Two neurons responded to bending anywhere along the setal shaft. None of the four tested neurons responded to bending after the distal half of the seta was removed.

Bend neurons were sensitive to changes in osmolarity (Fig. 10). All tested neurons ($n$ = 11) responded with high-frequency spiking to pulses of deionized water. The response to bending did not change after stimulation with 8-s pulses of deionized water. Three neurons were kept in deionized water for a prolonged period, and they all stopped responding to the deionized water after 1–2 min. One neuron spiked constantly for 1.5 min before it stopped responding. These three neurons showed a profound reduction in responsiveness to bending before they stopped responding. None of the three neurons responded to bending after 5 min in deionized water, and none of them recovered after 30 min in full-strength seawater.

Bend neurons differed in their responses to the salinity treatments. Four bend neurons from maxilliped 3 were tested with a set of seawater stimuli at different osmolarities—1.75% to 5.25% salt concentration. (Full-strength seawater is 3.5%, so these range from 50% to 150% of normal seawater; Fig. 10B). One neuron responded most strongly to hyperosmotic stimuli (Fig. 10B, neuron 1); one neuron responded only to hyposmotic stimuli (Fig. 10, neuron 2); and two neurons responded in similar ways to hypo- and hyperosmotic stimuli (Fig. 10, neurons 3–4), but with different intensities. The response to changes in salinity showed a response latency of several seconds, even when the neurons were exposed to deionized water (Fig. 10A).

### *Tactile neurons from cuspidate setae*

The 10 tactile neurons obtained from cuspidate setae were highly sensitive, responding to the slightest touch by the probe that caused no visible setal movement (Fig. 11A). Eight of the neurons gave phaso-tonic responses to prolonged displacement (Fig. 11B): these neurons tended to adapt similarly to bend neurons (Fig. 11C). Sensitivity to direction, amplitude, or velocity of mechanical stimulation was not examined because stimulation was necessarily performed by hand and therefore was not accurate enough for such quantification.

The tactile neurons were not sensitive to pulses of deion-

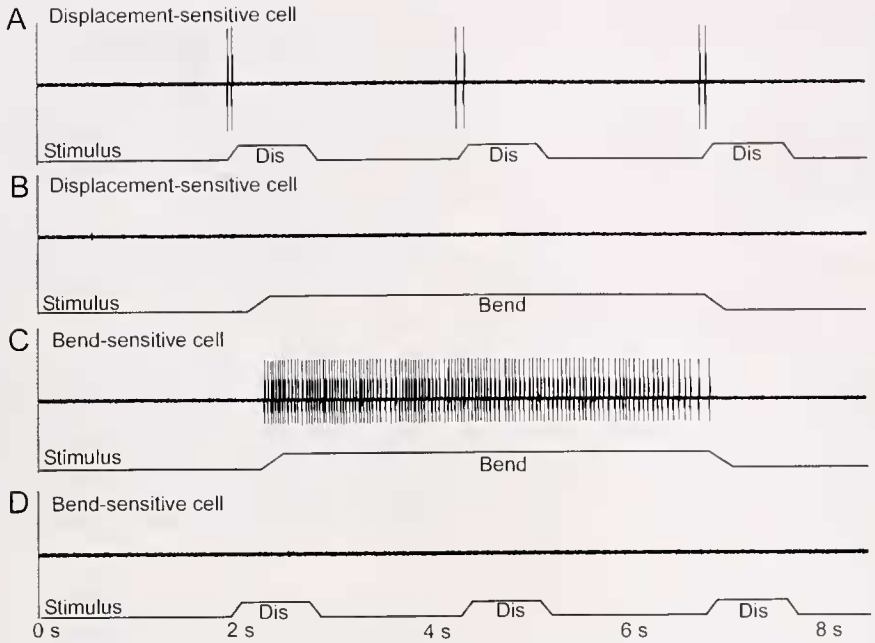


**Figure 3.** Typical response characteristics of the two types of mechanosensory neurons from simple setae. (A) and (B): A displacement-sensitive neuron. (A) The neuron responded phasically to a 1-s displacement. Note that the spikes occurred only during the displacement and not during the stationary state. (B) The neuron from A did not respond to prolonged bending. (C) and (D): A bend-sensitive neuron. (C) The neuron responded phaso-tonically during the entire 5 s of bending. (D) The neuron from C did not respond to displacement.

ized water. In one neuron, the cuticle was opened by cutting (with a pair of scissors) the seta at the midpoint along the setal shaft. This neuron continued to respond to tactile stimuli and began to respond to pulses of deionized water.

## Discussion

Two types of mechanosensory neuron from the simple setae on the mouthparts of *Panulirus argus* were demonstrated in this study: displacement-sensitive neurons and bend-sensitive neurons. Furthermore, highly sensitive "tactile" neurons were found in the cuspidate setae. The identification of bend-sensitive neurons was one of our most significant findings; such neurons have not been previously demonstrated for any arthropod seta. Our results, taken together, clearly show that the mechanosensory input during feeding is more complex than previously believed (Altner *et al.*, 1983).

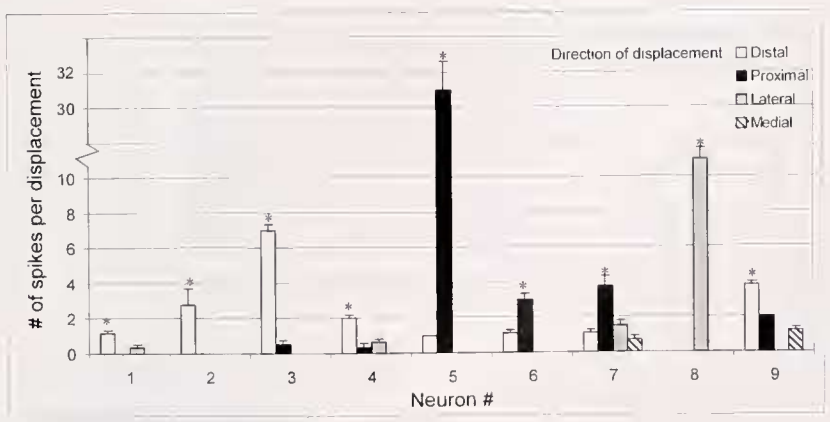


**Figure 4.** Directional sensitivity of nine displacement neurons. Only neurons 2 and 8 responded exclusively to displacement in one direction, but all nine neurons had a "best" direction that produced the most action potentials. The "best" directions tended to be proximal or distal. Responses marked with an asterisk are significantly larger than those to the other directions (ANOVA with Tukey's *post hoc* tests, $P < 0.05$). The directions are relative to the long axis of the limb. Values are means ± SEM, $n = 6–8$ (repeated stimulations of the same neuron).

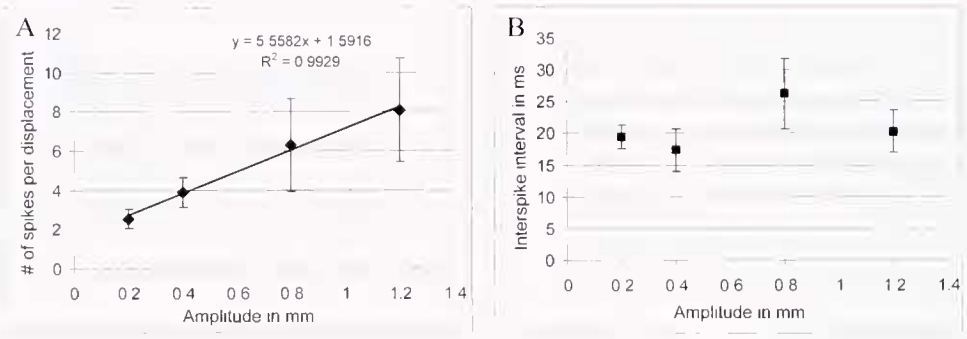


**Figure 5.** Amplitude sensitivity of displacement neurons. (A) Response of displacement neurons, in spikes per displacement, increased with stimulus amplitude. Note that the stimulus amplitude refers to the distance traveled by the manipulatory hook and that the distance traveled by any given part of the seta was not linear but followed a sine curve (see Materials and Methods for details). A best-fit regression line is drawn through the data points, and the regression equation and coefficient of determination ($R^2$) are shown above it. (B) The mean interspike interval was not influenced by changes in the stimulus amplitude. Values are means ± SEM, $n = 8$ (8 neurons were tested with each amplitude, but the value from each neuron was a mean of 10 stimulations).

*Bend-sensitive neurons*

Several observations support bend-sensitivity. First, most of the bend neurons did not respond to large displacements, and the few that did gave a very small response—much smaller than to bending. In addition, six out of eight neurons did not respond to bending of the proximal half of the seta, showing that distal distortion is needed to activate most of the bend neurons. Finally, none of the bend neurons responded after the distal part of the setal shaft was removed, whereas all the displacement neurons kept responding after the ablation. This again shows that the sensitive part of most of the bend neurons lies within the distal half of the seta. We therefore conclude that the division of the mechanosensory neurons into bend- and displacement-sensitive neurons is a real property and not a stimulation artifact.

This is the first demonstration of bend sensitivity among mechanosensory neurons in arthropod setae; only displacement sensitivity has been found in earlier studies (Wiese, 1976; Vedel and Clarac, 1976; Tazaki, 1977; Janse, 1980; Tautz *et al.*, 1981; Solon and Kass-Simon, 1981; Altner *et al.*, 1983; Vedel, 1985; Heinisch and Wiese, 1987; Crouau, 1995; Keil, 1998). Crouau (1989) suggested that the plumose setae from the antenna of the mysid *Antromysis juberthiei* are bend sensitive but with neurons responding to both bending and displacement; no experimental evidence was provided for this suggestion.

Simple setae are likely to bend during food handling by the mouthparts when prey is grasped and pressure is applied directly to the tip of the setae. The setae do bend during food

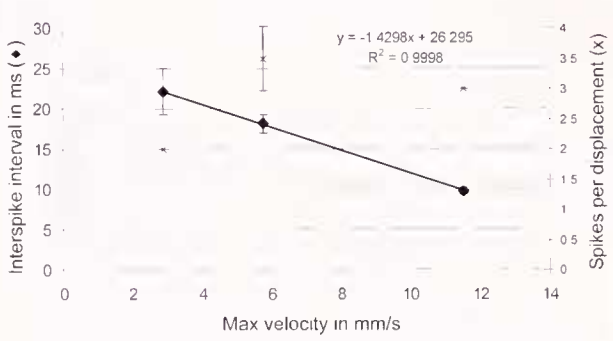


**Figure 6.** A displacement-sensitive neuron showed a decline in mean interspike interval with higher velocities (diamond symbols). The values are means ± SEM, $n = 10$. The line indicates the best-fit linear regression. The equation and coefficient of determination ($R^2$) are shown above the line. The number of spikes did not change with changes in velocity (X-shaped symbols). Note that the velocity is given for the manipulatory hook and that the angular velocity followed a sine curve (see Materials and Methods for details). The values refer to the maximum velocities of the seta.

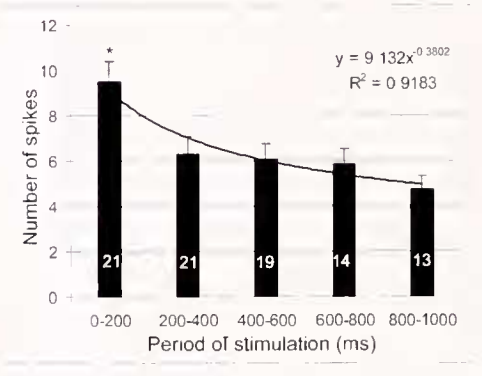


**Figure 7.** Adaptation of the phaso-tonic response of bend neurons. Values are means ± SEM; $n$ is written in each bar. The reason for the decline in $n$ values is that the neurons were stimulated for different periods. The asterisk indicates that the responses in the first period were significantly larger than the responses in the subsequent periods (ANOVA with Tukey's *post hoc* test, $P < 0.02$). All of the neurons displayed a slow adaptation to prolonged bending, seen as a decline in spiking frequency. The equation is the best-fit regression line, and $R^2$ is the coefficient of determination.

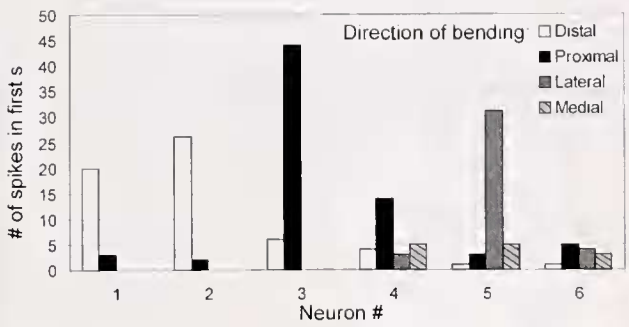


**Figure 8.** Six of ten tested bend neurons were directionally sensitive, responding with more spikes when bent in one direction than in others. The given direction of bending is relative to the long axis of the appendage. None of the six neurons responded exclusively to one direction of bending, but in general they showed a "best" direction. Neuron 6 was different in that it seemed to display a "worst" direction. No error bars are given since $n = 1$ for all recordings.

manipulation (Fig. 2), and this should activate the bend-sensitive neurons. As seen in video recordings, the distal part of the seta is most likely to bend during food manipulation, consistent with the fact that most bend neurons are only sensitive to bending distally (Fig. 9). Decapods in general have mandibles with separate areas for biting or crushing the prey (incisor and molar processes, respectively) (Lavalli and Factor, 1992; Garm and Høeg, 2001). Bend sensitivity, perhaps in coordination with proprioceptors, may provide animals with information on the hardness of the prey, affecting the decision about whether to crush or bite the prey item with the mandibles. The phaso-tonic response of bend neurons should ensure that the animals get information on the position of the object even when the prey is not moving or being moved. The directionality and region of sensitivity of bend neurons should give information on shape, texture, and location of the prey item, in addition to the stimulus direction and velocity information provided by displacement neurons (discussed below).

An interesting question is how the directional sensitivity of the bend neurons is enabled. It could be due either to the mechanical properties of the setal cuticle making bending more likely in one or more directions, or to the morphological arrangement of neurons inside the setal lumen. We did not examine the mechanical properties of the setae in any detail; but since the recorded responses are all to the same degree of bending (approximately 45°), stiffness of the setae cannot account for the observed directionality. We therefore believe that the arrangement of the outer dendritic segments is causing the directionality of some of the bend neurons. Normally the sensory cilia are arranged in a ciliary compartment enclosed by a dendritic sheath with no noticeable order or orientation, but this may be different for these

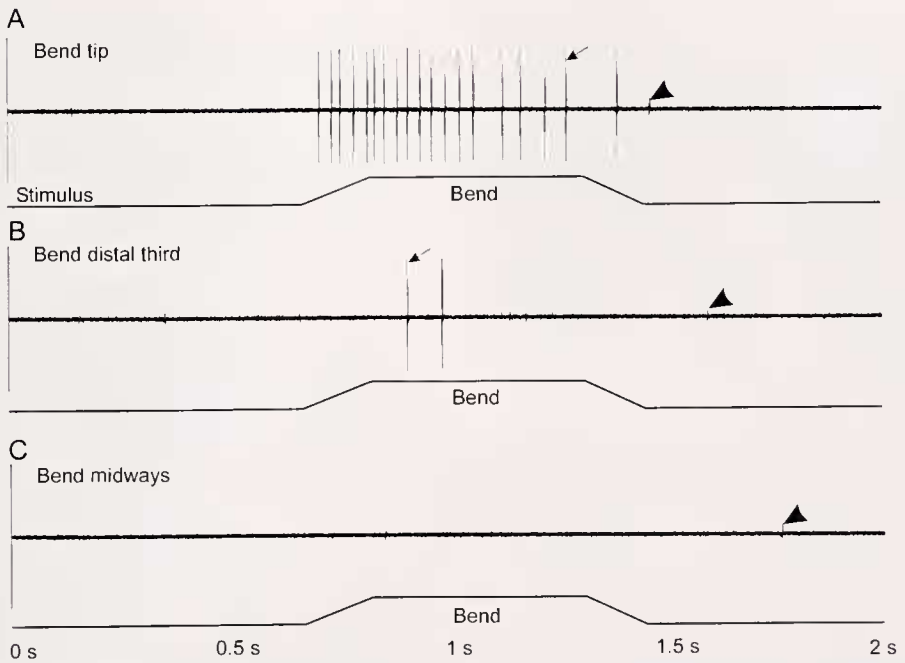


**Figure 9.** Responses from a bend neuron (arrow) to bending at different regions of the setal shaft. (A) When the seta was bent close to its tip, the neuron responded phaso-tonically throughout the entire period of bending. (B) When the seta was bent in the region about a third of the way from the tip, the neuron responded phasically with only two spikes. (C) This neuron, similar to five of the other bend neurons tested for region-sensitivity, did not respond to bending at the proximal half of the setal shaft. Arrowheads indicate responses from unidentified neurons.

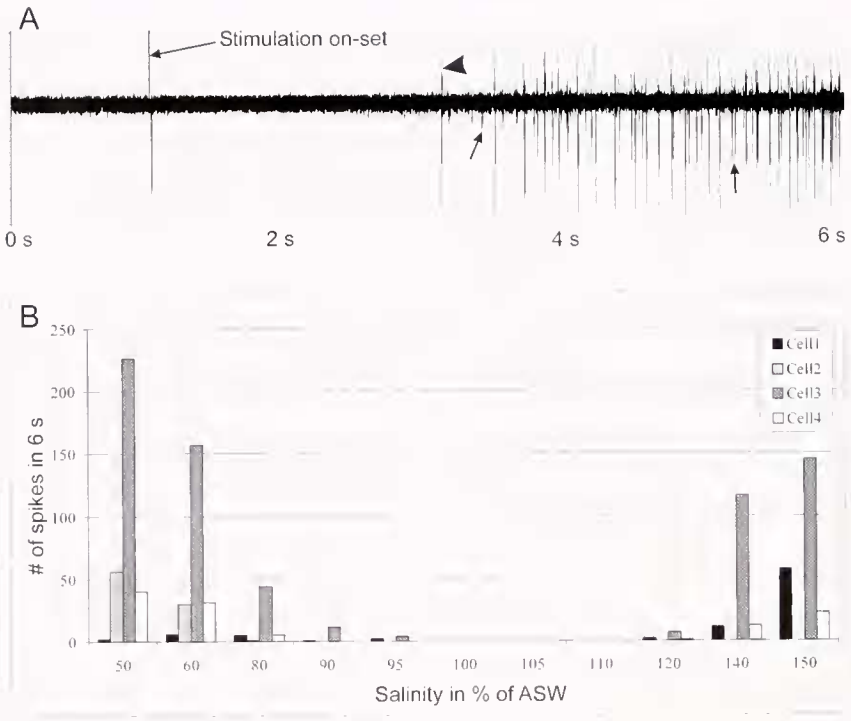


**Figure 10.** Bend neurons were sensitive to osmolarity. (A) Response to an 8-s pulse of deionized water. The response had a typical latency of a few seconds. (B) Response of four bend neurons to changes in osmolarity. Note that neuron 2 responded only to hypo-osmolarity, and neuron 1 mostly to hyper-osmolarity. The percentage given is relative to the response to full-strength seawater (3.5% salinity). The 6-s spike count started at the first spike.

directionally sensitive bend neurons. We must also ask how the ultrastructural arrangement ensures that most of the bend neurons were sensitive only to bending of the distal half of the seta. This might result from the transition zone between the inner and outer dendritic segment lying midway in the shaft, as it does for some aesthetasc setae (Ache, 1982). Since the outer dendritic segment is assumed to be the receptive part (Schmidt and Gnatzy, 1984; Crouau, 1994, 2001), such an arrangement would make the proximal part of the seta insensitive.

*Displacement-sensitive neurons*

Except for the higher amplitude threshold, the physiological properties of displacement-sensitive neurons in simple setae on the mouthparts of *P. argus* are similar to many, though not all, previously described mechanosensors on other body parts from a variety of crustaceans. We show that the amplitude of displacement is encoded in the number of action potentials produced and the velocity/acceleration in the firing frequency. This is in good concordance with earlier findings for mechanosensory neurons from crustaceans (Wiese, 1976; Tautz *et al.*, 1981; Altner *et al.*, 1983; Derby, 1989; Fields *et al.*, 2002). The function of displacement-sensitive neurons has been suggested to be sensing vibrations and thereby detecting prey, predators, or conspecifics from a distance (Wiese, 1976; Tazaki, 1977; Tautz *et al.*, 1981; Masters *et al.*, 1982; Vedel, 1985). However, this is probably not the case for the displacement-sensitive neurons from mouthpart setae. These neurons are directly involved in coarse manipulation of food and are therefore more likely to collect tactile information about the food items. This means that their dynamic range should be biased towards high-amplitude stimulation, which correlates well with our results. For example, the angular sensitivity thresholds of 4–6° reported here are higher than previously reported thresholds from displacement neurons. Mechanosensory neurons from the plumose setae of other decapod crustaceans have thresholds down to 0.01° (Wiese, 1976), and there are indications of even lower thresholds in copepod antennae (Fields *et al.*, 2002). Mechanosensory neurons of insects and spiders also have lower thresholds than we report here (Keil, 1998; Barth and Höller, 1999; Cokl and Virant-Doberlet, 2003). This difference in thresholds again supports the functional difference between mouthpart setae and setae found on other structures believed to be specialized motion detectors.

The detailed response pattern of mouthpart displacement neurons probably adds significantly to the information gath-

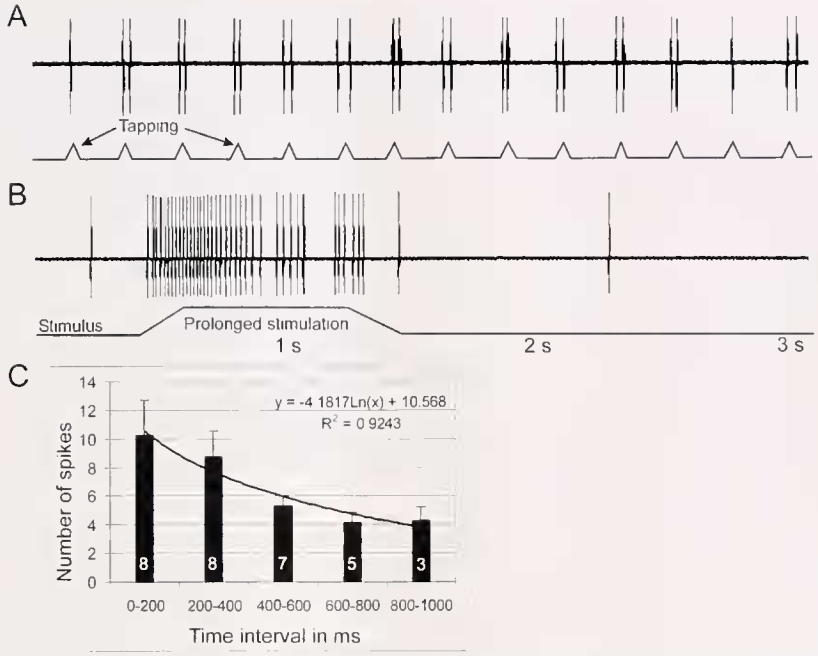


**Figure 11.** "Tactile" neurons from cuspidate setae. (A) Tapping the setae caused no visible movements of the seta, but produced one to two spikes per stimulation. (B) Example of phaso-tonic response to prolonged stimulation. (C) The phaso-tonic neurons from cuspidate setae tended to adapt slowly to prolonged stimulation, but the responses were not significantly different at the 0.05 significance level (ANOVA). The line is the best-fit regression; the line equation and coefficient of determination are shown. Values are means ± SEM; *n* is indicated in bars. The decline in *n* values is due to the neurons being stimulated for different periods.

ered about the prey items during feeding. If a living prey held by the mouthparts tries to escape, the directional sensitivity of the displacement neurons could indicate the direction of the movement. The amplitude- and velocity-sensitive neurons could give further detailed information about the movements of the prey.

### *Tactile neurons from cuspidate setae*

Tactile neurons from cuspidate setae give phaso-tonic spiking responses, and they have very low response thresholds as indicated by their responsiveness to very small movements. This is not surprising since cuspidate setae have a much reduced socket and can hardly pivot in this socket (Vedel, 1985). Cuspidate setae are situated on the very distal or medial edge of the mouthparts and will therefore make the initial contact with prey. They are the setae most involved in the actual holding of the prey (Garm, 2004). Consequently, the tactile neurons could provide information about when contact is made, and possibly also about the texture of the prey, by correlating the amplitude of the displacement with information from internal proprioceptors. The responsiveness is similar to that described for mechanosensory neurons in cuspidate setae referred to as "spines" on antenna 2 of *Panulirus vulgaris* (Vedel, 1985).

### *Combined mechanosensory function of mouthpart setae*

The array of mechanosensory input from the mouthpart setae described by our experiments could be viewed as a somatosensory system that provides detailed information about the shape, size, texture, position, and movements of prey items. The spatial resolution should also be considerable, since the setae are closely packed on most parts of the food-handling areas. The acquisition of such detailed information during food handling conflicts with an earlier suggestion about the amount of tactile information gathered during feeding. Mechanosensory neurons on the chelae of *Austropotamobius torrentium* were suggested to provide only crude information on the presence or absence of food (Altner *et al.*, 1983). On the other hand, behavioral studies of other decapods support the notion that detailed information is available to the animals. When squat lobsters (*Munida sarsi* and *M. tenuimana*) and shrimp (*Palaemon adspersus*) handle prey, the flexible and variable mouthpart movements are performed with high speed and precision (Garm and Høeg, 2001; Garm *et al.*, 2003). Such movements can only be performed with detailed somatosensory input.

### *Osmosensitivity of mouthpart mechanosensory neurons*

Sensitivity to changes in osmolarity is known from behavioral experiments on some decapod crustaceans, such as

the clawed lobster *Homarus americanus* (Jury *et al.*, 1994; Dufort *et al.*, 2001). Moreover, both chemosensors (Derby, unpubl. data) and mechanosensors (Tazaki, 1975) of spiny lobsters can be sensitive to stimulus osmolarity. Schmidt (1989) also found osmosensitivity on the walking legs of *Carcinus maenas*, but did not show other modalities of these neurons. We have shown that bend-sensitive neurons respond to salinity changes, with some neurons responding only to hyposmotic stimuli, some mainly to hyperosmotic stimuli, and some to both. Differential responses such as these could be the underlying sensory mechanism for behavioral responses to osmotic stimuli. Similar bimodal properties have been reported from osmosensory and mechanosensory neurons in tactile setae of the antennae of the spiny lobster *Panulirus japonicus* (Tazaki, 1975). Interestingly, the bimodal neurons in *P. japonicus* were described as being sensitive to displacement, but the method of mechanical stimulation used by Tazaki (1975) was such that bending during displacement may have occurred.

Many interesting questions stem from the finding of bimodal neurons that are sensitive to both mechanical and osmotic stimulation. First, what is the primary modality of these neurons, and is the secondary modality merely noise in the animal's sensory input? Due to the diversity of the detailed bend response, we believe that the neurons are primary bend neurons. Since the osmoresponse is also complex and contains information about osmolarity, we find it likely that the neurons are truly bimodal and that they probably convey both types of information. The sensitivity of the bend neurons to osmolarity could mediate the observed behavioral responses to salinity changes, but such a sensory system would be much more effective in detecting salinity changes from a distance if it were situated on the long antenna 2, as also indicated by Tazaki (1975). Alternatively, mouthpart osmoreceptors might provide information about the chemical quality of prey items. *Panulirus argus*, like most decapods, is partly a scavenger, and the osmolarity of decaying prey changes due to metabolites produced by the actions of microorganisms and due to the breakdown and solubilization of insoluble macromolecules (R. Glud, Institute of Biology, University of Copenhagen; *pers. comm.*). But whether these processes will result in osmotic changes large enough for the neurons to detect is questionable. Furthermore, a latency of more than 2 s also seems to obscure the function, since the prey will often be at least partly ingested in this time frame. It is therefore not obvious to us what information may be conveyed by the osmosensitive neurons.

Bimodal receptor neurons are not common but have been found in molluscs and crustaceans. Bimodal chemosensory and mechanosensory neurons have been found in the crayfish *Austropotamobius torrentium* and in the opisthobranch gastropod *Tritonia diomedea* (Audesirk and Audesirk, 1980; Hatt, 1986). In the case of *Tritonia*, bimodality is suggested to be due to peripheral synapses between unimodal afferents (Audesirk and Audesirk, 1980). The caudal photoreceptor of crayfish offers another example of bimodal sensory neurons responding to both mechanical and photostimuli; in this case the primary modality is believed to be photosensation (Pei *et al.*, 1996).

We are intrigued by the finding that only bend neurons respond to changes in osmolarity. One possible explanation is that the morphological arrangement of mechanosensory neurons in these setae is such that only bend neurons are exposed to the external environment. This idea is supported by the observation that after the cuspidate setae were amputated halfway up the shaft, the tactile neurons within them could be made to respond to deionized water. Morphological studies are needed to verify this hypothesis.

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